Incidence and Severity of Cavity Spot of Carrot as Affected by Pigmentation, Temperature, and Rainfall

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Abstract

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Field trials to determine the effect of carrot pigmentation and weather parameters on cavity spot (CS) of carrot were conducted in the Holland/Bradford Marsh region of Ontario between 2002 and 2009. In all, 23 colored carrot cultivars from the United States Department of Agriculture (USDA) Agricultural Research Service breeding program at the University of Wisconsin ($n = 5$) and commercial seed companies ($n = 18$) were seeded in organic soil (pH 6 to 7, 45 to 75% organic matter) in late May to early June and harvested in late October or early November. Carrot roots were assessed for CS severity midseason and postharvest. Evaluations postharvest indicated that the purple pigmented carrot from breeding line 'USDA 106-3' and cultivars 'Purple Rain' and 'Purple Haze' consistently had low CS severity. The orange-pigmented 'USDA 101-23', 'Cellobunch', 'YaYa', and 'Envy'

had moderate CS; and the red-pigmented carrot breeding line 'USDA 104-3' and cultivars 'Atomic Red', 'Proline Red', 'Dragon', and an unnamed line from India had high CS. Differences in CS severity in carrot cultivars between evaluations at midseason and postharvest suggest that some carrot cultivars are more susceptible to *Pythium* spp. inoculum in soil (alloinfection) and others to secondary infection (autoinfection) that can be attributed to the *Pythium* sp. involved in CS. CS severity was positively correlated with total rainfall 2 and 3 months after seeding, and was negatively correlated with number of days with air temperature $\geq 30^{\circ}\text{C}$ 3 and 4 months after seeding. Soil temperature and total rainfall were the best predictors of CS incidence and severity. These results could allow a forecast of disease incidence and severity at harvest.

Carrot (*Daucus carota* L. subsp. *sativa* Hoffm. (Arcang.)) is produced on both organic and mineral soils in North America, including Ontario, Canada, for fresh market and for processing. Most of the carrot cultivars are orange pigmented but cultivars with other pigments and colors, such as purple, red, dark orange, yellow, and white, are being gradually introduced into local markets, with high consumer acceptance. Cavity spot (CS) is an important limiting factor in carrot production worldwide, including Ontario (11,13,18,28,38). Although the disease does not reduce harvested tonnage, carrot roots with more than a few superficial cavities are not accepted for fresh market or for processing, which results in reduced marketable yield (28).

CS is characterized by small, sunken, elliptical, olivaceous lesions on carrot roots, normally oriented horizontally across the root. The lesions can cover the entire taproot or be concentrated on the upper third of the root. Lesions become elongate and darken with time and, depending on environmental conditions, may reach up to 2 cm in length and 1-5 mm in depth (3,35,48,49). CS does not induce any visible symptoms on the aboveground plant parts (13,46).

A complex of *Pythium* spp. that differs from region to region is involved in CS on carrot. Although the slow-growing *Pythium violae* Chesters & Hickman and *P. sulcatum* R.G. Pratt & J.E. Mitch. are most often associated with the disease, other species such as *P. sylvaticum* W.A. Campb. & F.F. Hendrix, *P. ultimum* Trow, *P. irregulare* Buisman, *P. intermedium* de Bary, and *P. aphididermatum* (Edson) Fitzp. have also been isolated from CS lesions (3,28,46,48,49). First reported by Guba et al. (13) on carrot and parsnip in Massachusetts, CS is now present in California and Michigan, the two major carrot producers in the United States (23).

In Canada, CS has been reported in British Columbia (3), Quebec (2), and Ontario, particularly in the Bradford area, where one-half of the carrot production in the province is located (28,31). *P. sulcatum*, *P. ultimum*, and *P. irregulare* are commonly isolated from carrot grown on organic soils in the Bradford area (28). The disease is currently managed by using cultural practices such as avoiding fields with a history of CS, growing carrot cultivars on raised plant beds (19), and applying fungicides. Registered products include metalaxyl (Ridomil; Syngenta Crop Protection), an acylalanine (phenylamide) compound that is a systemic fungicide with activity against oomycetes (8,18,25,26,33); and cyazofamid (Ranman; ISK Biosciences Corporation), a phenylimidazole compound with activity against a broad spectrum of oomycetes at very low use rates (33). Management of agronomic aspects of production such as irrigation, soil cultivation, and the length of time crops are grown may all be used to reduce CS; in addition, selecting carrot cultivars with some field resistance may also be beneficial (7).

Research on the roles of plant pigments in improving human health, including carrot roots with different pigments, has been receiving special attention. There has been recognition of the antioxidant activities of α - and β -carotene in orange carrot roots, anthocyanins in purple roots, lutein in yellow roots, lycopene in red roots, and high fiber content in white roots, all of which contribute to improving human health (1,45). In addition to potential health benefits, consumers enjoy pigmented carrot roots for their attractive colors and for the pleasant flavors induced by sugars and essential oils of various pigmented cultivars (10,12,16,39). Studies have been conducted to evaluate the antioxidant capacity of pigmented carrot cultivars and how the antioxidants are affected by carrot genotype, storage, and production systems, (1,6,9,10,21), but very few studies have been conducted on the effects of pigments on pests or diseases, including CS (5).

An 8-year field study was conducted in the organic soils of the Holland Marsh at the Muck Crops Research Station (MCRS), Bradford, Ontario, to investigate the response of several pigmented carrot cultivars to CS. The objectives of the study were to (i) evaluate the incidence and severity of CS with different pigmentation

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and (ii) evaluate the influence of weather factors, particularly rainfall and temperature during the growing season, on CS severity on cultivars with different pigmentation.

Materials and Methods

Field plots establishment. Field trials were conducted on organic soil in the Holland/Bradford Marsh (44° 15' N, 77° 35' W), Ontario, Canada, at the University of Guelph MCRS from 2002 to 2009. The organic soil, a typic Hemic-Histosol, contained 45 to 75% organic matter with a pH of 6.0 to 7.0. *Pythium* spp. that cause CS occur naturally in these soils (28).

Carrot breeding lines and cultivars. Carrot breeding lines with different pigments were provided by the United States Department of Agriculture–Agricultural Research Service (USDA-ARS) breeding program at the University of Wisconsin. These breeding lines were white, yellow, red, purple, and dark orange carrot roots, and were evaluated from 2002 to 2009, with the exception of 2007. The carrot breeding lines were compared with ‘Cellobunch’ carrot (Seminis Vegetable Seed), a popular cultivar with Ontario growers, in the evaluations from 2003 to 2009. In addition, 18 pigmented carrot cultivars—orange ($n = 4$), purple ($n = 4$), red ($n = 4$), white ($n = 2$), yellow ($n = 4$), and 1 with mixed color—were evaluated from 2005 to 2009 (Table 1). The cultivars included in our study varied from year to year due to seed availability.

Carrot cultivars were direct seeded on raised plant beds using a push V-belt seeder (70 to 80 seeds/m) on 28 May and 6 June 2002, 30 May 2003, 27 May 2004, 31 May 2005, 30 May 2006, 29 May 2007, 2 June 2008, and 1 June 2009. The experiments were arranged in a randomized complete block design with four replications per treatment. Each experimental unit consisted of two rows (86 cm apart) that were 5 m long from 2002 to 2006 and 6 m long from 2007 to 2009. Fertilizer was applied according to Ontario Ministry of Agriculture Food and Rural Affairs (OMAFRA) recommendations (33) based on each year’s preplant soil evaluations for phosphorus and potassium. Weeds and insects were controlled according to OMAFRA recommendations (32,33). Plants were irrigated shortly after seeding if the soil was too dry to allow seed to germinate.

CS assessments. The carrot growing season was divided into 30-day periods (months) after carrot seeding for a total of 5 months. Midseason assessments occurred between July and Sep-

tember, about two and half to 3 months after planting (MAP). These assessments were conducted on breeding lines from 2004 to 2009, except in 2007, when the breeding lines were not evaluated, and on cultivars from 2005 to 2009, although, in 2009, there were not enough carrot roots for midseason evaluation of all cultivars, due to poor germination. Assessments were also done after carrot roots were harvested, about 5 MAP, and placed in a cold storage that was maintained at a temperature of $1 \pm 1^\circ\text{C}$ and relative humidity of $95 \pm 2\%$. For the midseason evaluations, a random sample of 25 consecutive carrot roots in one row of each replicate plot was hand harvested and assessed. Midseason assessments were carried out on 27 July 2004, 4 August 2005, 16 August 2006, 16 August 2007, 25 August 2008, and 10 September 2009. Carrot roots were hand harvested between 22 October and 5 November from 2002 to 2009. In all, 25 (2002 to 2004) and 50 (2005 to 2009) consecutive carrot roots were harvested from each replicate, placed into netted bags, and kept in cold storage maintained at the same temperature and relative humidity as above, until carrot roots were assessed for CS. Disease assessments were conducted on 5 December 2002; 8 December 2003; 9 December 2004; 23 November 2005; 27 November 2006; 11 December 2007; 4 and 5 December 2008; and 22, 23, and 24 December 2009 and 4 January 2010, about 4 to 6 weeks postharvest.

Carrot roots were washed with cold water in a small drum washer, air dried at room temperature (23 to 25°C), and examined for presence and size of lesions and the percentage of roots covered with lesions (disease incidence [DI]). Carrot roots from each replicate plot were grouped into six severity classes based on the length of horizontal lesions, where class 0 = no lesions, class 1 = lesions of 0 to 0.9 mm, class 2 = lesions of 1 to 2 mm, class 3 = lesions of 2 to 5 mm, class 4 = lesions of 5 to 10 mm, and class 5 = lesions >10 mm. The severity values were transformed to an index with a 0-to-100 scale using a modified formula of Kobriger and Hagedorn (22). The number of carrot roots in each severity class was multiplied by the severity class value (0 to 5) and the results from each severity class were summed. The obtained value was divided by the total number of carrot roots examined, multiplied by the number of severity classes minus 1 (5), and then multiplied by 100. This resulted in a disease severity index (DSI) equation: $\text{DSI} = [\sum(\text{class number}) \times (\text{number of roots in each class})] / (\text{total number of roots} \times \text{number classes} - 1) \times 100$.

Table 1. Colored carrot breeding lines, and commercial cultivars grown at the Muck Crops Research Station, Holland Marsh, Ontario, and evaluated for cavity spot caused by *Pythium* spp. from 2002 to 2009^y

Carrot breeding line or cultivar ^z	Source or seed company	Carrot color	Years evaluated
Belgian White	Bountiful Gardens. Willits, CA	White	2005–2006, 2008
Crème de Lite	Nunhems. Brooks, OR	White	2007–2008
USDA 105-7	USDA-ARS, University of Wisconsin	White	2002–2006, 2008–2009
White Satin	Bejo Seed Inc. Geneva, NY	White	2007–2009
Amarillo Yellow	Bountiful Gardens. Willits, CA	Yellow	2005–2006, 2008
Mellow Yellow	Bejo Seed Inc. Geneva, NY	Yellow	2005–2009
USDA 102-1	USDA-ARS, University of Wisconsin	Yellow	2002–2008, 2009
Yellow Stone	Garden City Seeds. Ellensburg, PA	Yellow	2005–2006, 2008
Alpha Better F1	Alpha Seeds. South Africa	Orange	2007–2008
Cellobunch	Seminis Vegetable Seed Oxnard, CA	Orange	2003–2009
Envy	Seminis Vegetable Seed Oxnard, CA	Orange	2007–2009
YaYa	Bejo Seed Inc. Geneva, NY	Orange	2005–2008
USDA 101-23	USDA-ARS, University of Wisconsin	Dark orange	2002–2006, 2008–2009
Atomic Red	Johnny’s Selected Seeds. Winslow, MA	Red	2005–2009
Dragon	Garden City Seeds. Ellensburg, PA	Red	2005–2006, 2008
Proline Red	India	Red	2008
Unnamed Indian	India	Red	2007–2008
Cosmic Purple	Johnny’s Selected Seeds. Winslow, MA	Purple	2005–2008
Purple Haze	Bejo Seed Inc. Geneva, NY	Purple	2005–2009
Purple Rain	Bejo Seed Inc. Geneva, NY	Purple	2007–2008
USDA 106-3	USDA-ARS, University of Wisconsin	Purple	2002–2006, 2008–2009
Rainbow	Bejo Seed Inc. Geneva, NY	Mixed	2005–2006

^y Trials were conducted on organic soil, a typic Hemic-Histosol with 45 to 75% organic matter and pH 6.0 to 7.0 on the Holland/Bradford Marsh (44° 15' N, 77° 35' W), Ontario, Canada.

^z Carrot breeding line source: United States Department of Agriculture–Agricultural Research Service (USDA-ARS) breeding program at the University of Wisconsin.

Measurement of weather variables. Air temperatures (maximum, minimum, and average) and relative humidity were assessed every minute using a probe (HMP 35C). Soil temperature (°C) at 5-, 10-, and 20-cm depths was measured using a 107-B probe and total rainfall (mm) was measured using a tipping bucket rain gage (TE525). Weather parameter instruments were connected to a data logger (CR 10X; Campbell Scientific Inc.) at a weather station located approximately 200 m from the carrot plots. Data including air temperature, soil temperature, and total rainfall collected from May to November of each year were combined into five monthly periods from the date that carrot roots were planted until harvest. Likewise, the number of days with precipitation ≥ 2.5 mm and the number of days with air temperatures $\geq 30^{\circ}\text{C}$ (hot days) (47) were calculated. The established monthly periods corresponded to calendar days as follows: Month one (M1) = late May through June, month two (M2) = July, month three (M3) = August, month four (M4) = September, and month five (M5) = October through the first week of November. Midseason CS evaluations were conducted between M2 and M3 after planting.

Statistical analysis. DI and DSI data were assessed for normality using the Shapiro-Wilk test for residuals. Outliers were identified using the Lund's test of standardized residuals (24). For both Wisconsin breeding lines and carrot cultivars, data were combined and compared with the standard orange carrot Cellobunch for the 2004 to 2009 evaluations of the breeding lines and for the 2005 to 2009 evaluations of the commercially produced carrot cultivars. An analysis of variance was performed to partition the variance into effects of carrot cultivars and year on DI and DSI to identify interactions using PROC GLM procedures of SAS (version 9.2; SAS Institute). To identify the years that were most likely causing the interactions, the interactions were examined combining several years and eliminating other years from the analysis of variance. When the interaction was not significant, the data from the years were pooled and analyzed together and the years with significant interactions were analyzed individually.

All weather variables—maximum, minimum, and average air temperatures (°C); air temperatures $\geq 30^{\circ}\text{C}$; soil temperatures (°C) at 5, 10, and 20 cm; average soil temperature between 5 and 10 cm and between 5, 10, and 20 cm in depth; total rainfall (mm); and number of days with precipitation ≥ 2.5 mm—were evaluated for their association with CS incidence and severity using Pearson's correlation coefficients. A stepwise regression procedure was used to identify the best combination of variables that most influenced CS incidence and severity and to generate predictor models. Stepwise regressions were performed using PROC REG with the significance level to enter the model being $P = 0.15$ and the significance level to stay in the model being $P = 0.10$. Statistical analysis was conducted using PROC PLOT, PROC CORR, PROC REG, and PROC Univariate. For the analysis of variance, means were

separated using Tukey's Studentized range (honestly significant difference) test at $P = 0.05$.

Results

***Pythium* spp. and CS.** *P. ultimum*, *P. irregulare*, *P. aphanidermatum*, *P. violae*, and *P. intermedium* were isolated from carrot roots with CS symptoms between 2007 and 2009. Lesions were 1 to 10 mm in length and occurred along the entire taproot but were most abundant on the upper third of the root. There was a similar trend for DI and DSI in the assessment of susceptibility to CS; therefore, only DSI data are presented. For the evaluation of weather parameters in relation to CS, both DI and DSI were considered.

Carrot breeding line CS assessments. There was no interaction between lines and year for the midseason assessment; thus, DSI data were pooled and averaged (Table 2). Purple, dark orange, and red lines and Cellobunch had very low DSI values of 3.7, 6.9, 8.0, and 9.1, respectively. The DSI was relatively high and similar for the white (20.3) and yellow (17.8) breeding lines (Table 2).

Overall, CS DSI was higher in 2004 than other years, according to post-harvest assessments. A significant carrot breeding line–year interaction for CS severity ($P = 0.014$) was observed for DSI in 2002, 2003, and 2004; thus, carrot breeding lines and CS were evaluated individually by year for these years. There was no year–line interaction for 2005, 2006, 2008, and 2009 ($P = 0.6393$); therefore, these data were combined and the DSI averaged (Table 2). When CS was evaluated by year, the purple carrot line 'USDA 106-3' consistently had low disease severity among all the breeding lines. In 2002, disease severity of the purple line was similar to that of the red, dark orange, and white lines whereas, in 2003 and 2004, the DSI of the purple line and the dark orange line 'USDA 101-23' were similar and, in 2004, Cellobunch also had a similar, lower DSI. The highest disease severity was recorded on the red line 'USDA 104-3' (43.8) in 2003 and on the white (61.4), yellow (59.8), and red carrot cultivars (51.2) in 2004. In 2002, only the yellow line had higher DSI than the purple cultivars (Table 2).

When the years 2005, 2008, and 2009 were combined, CS severity was low and similar for purple, yellow, white, and Cellobunch carrot, with DSI values of 19.2 to 30.4 (Table 2). CS severity was high and similar for the red (47.7) and dark orange (40.8) cultivars (Table 2).

Carrot cultivar CS assessments. Midseason assessments indicated that there was a significant cultivar–year interaction ($P < 0.0001$) among cultivars, and single-year effects were evaluated separately. In 2005 and 2007, there were no significant differences in CS severity among cultivars ($P = 0.324$, 2005; $P = 0.158$, 2007; Table 3). When significant differences in severity were observed, 'Purple Haze' carrot had the lowest CS severity. The yellow 'Mellow Yellow' carrot had higher DSI than Purple Haze in all years

Table 2. Cavity spot severity (disease severity index [DSI]) caused by *Pythium* spp. on colored carrot breeding lines and 'Cellobunch' grown on organic soil at the Muck Crops Research Station, Holland Marsh, Ontario, from 2002 to 2009^w

Breeding line or cultivar ^z	Carrot color	DSI midseason ^x		DSI postharvest ^y		
		2004–2008	2002	2003	2004	2005–2009
USDA 106-3	Purple	3.7 a	3.4 a	3.0 a	13.9 a	20.2 a
USDA 101-23	Dark orange	6.9 a	16.2 ab	18.2 ab	31.5 ab	40.8 bc
USDA 104-3	Red	8.0 a	23.5 ab	43.8 c	51.2 bc	47.7 c
USDA 105-7	White	20.3 b	24.3 ab	18.6 b	61.4 c	30.4 ab
USDA 102-1	Yellow	17.8 b	38.3 b	26.2 b	59.8 c	26.8 a
Cellobunch	Orange	9.1 a	...	...	27.9 ab	19.2 a

^w DSI = $[\Sigma(\text{class number}) \times (\text{number of roots in each class})] / (\text{total number of roots} \times \text{number classes} - 1) \times 100$, equation adapted from Kobriger and Hagedorn (22). Severity classes where class 0 = no lesions, class 1 = lesions of 0 to 0.9 mm, class 2 = lesions of 1 to 2 mm, class 3 = lesions of 2 to 5 mm, class 4 = lesions of 5 to 10 mm, and class 5 = lesions > 10 mm. Numbers in a column followed by the same letter were not significantly different at $P \leq 0.05$; ns denotes not significantly different at $P \leq 0.05$, based on Turkey's Studentized range (honestly significant difference) test.

^x Midseason = month two or three after planting. Carrot roots ($n = 25$ per replication) were hand harvested and evaluated for cavity spot severity. There were no data from 2007.

^y Carrot roots ($n = 25$ per replication in 2002–2004 and $n = 50$ per replication in 2005–2009) were harvested and kept in a cold storage ($1 \pm 1^{\circ}\text{C}$; relative humidity of $95 \pm 2\%$) for 4 to 6 weeks postharvest and assessed for cavity spot incidence and severity.

^z Carrot breeding lines source: United States Department of Agriculture–Agricultural Research Service (USDA-ARS) breeding program at the University of Wisconsin.

where differences were found (Table 3). In 2008, a number of other cultivars had higher DSI than Purple Haze, including white 'Crème de Lite', red 'Proline Red', orange 'Envy', and purple 'Cosmic Purple'. In 2009, red 'Atomic Red' and white 'White Satin' carrot also had higher DSI than Purple Haze.

Overall, there was an increase in CS severity between midseason and postharvest for most cultivars. A paired *t* test of CS severity ratings for midseason versus postharvest was significant for the 2005 ($P = 0.0026$), 2006 ($P = 0.0202$), and 2008 ($P = 0.0031$) assessments. In 2007 and 2009, CS severity ratings did not differ between the two assessments, perhaps due to low (2007) and high (2009) disease pressure during these years (Table 3). Nevertheless, a decrease of CS severity ratings from midseason to postharvest was recorded on the orange-pigmented Cellobunch (2006 and 2007), 'Alpha Better', and Envy (2007); the purple carrot Purple Haze (2006 to 2009) and 'Purple Rain' (2007 and 2008); the white Crème de Lite; and the yellow-pigmented 'Yellowstone' (2008) (Table 3).

When disease was assessed postharvest, a significant cultivar-year interaction for CS severity ($P = <0.0001$) was observed between 2005 and 2009; therefore, cultivar reaction was analyzed by year. All carrot roots had CS lesions but Purple Haze and Purple Rain had low levels of infection while a high incidence of infection was typically recorded on the red carrot roots. CS severity differed by year, and was high in 2009 and low in 2007.

Four cultivars were evaluated in all 5 years: Purple Haze, Cellobunch, Atomic Red, and Mellow Yellow. Purple Haze had a lower DSI than the other three cultivars, except in 2007, when overall disease severity was low (Table 3). There were no differences among any of these cultivars in 2007. Cellobunch had relatively low DSI, not different from Purple Haze, in all years except 2009, when overall disease severity was high. Mellow Yellow had a higher DSI than Purple Haze in all years except 2007. Disease severity of Atomic Red was higher than Purple Haze in every year except 2007 and it had a higher DSI than Mellow Yellow in 3 of the 5 years. Another purple-pigmented carrot, Cosmic Purple, was included in four of the years and had a higher DSI than Purple Haze, except in 2007. Orange Envy was included for 3 years and

the DSI was consistently similar to that of Cellobunch. In general, the red carrot cultivars had a high DSI, response of the yellow and white carrot cultivars was variable, and two of the purple cultivars were relatively resistant to CS (Table 3).

CS incidence and severity in relation to weather conditions.

Temperature and rainfall had major effects on CS. Average air temperatures were fairly consistent from year to year and similar to long-term average conditions for the area (Table 4). Rainfall amounts differed by year, with 2006 and 2009 being somewhat wetter than normal; 2005 and 2007 drier than normal; and 2002, 2003, 2004, and 2008 close to the long-term average rainfall. There were 52 days during the growing season with rainfall ≥ 2.5 mm in 2002, 63 in 2003 and 2006, 57 in 2004, 40 in 2005, 36 in 2007, 24 in 2008, and 29 in 2009 (Table 4).

Relationships between weather and disease severity. There was a significant and negative correlation between CS incidence (DI) and mean maximum temperature during M4 after planting (AP) ($r = -0.69$; $P = 0.05$; 21 to 26°C) and mean minimum air temperature during M5 AP ($r = -0.71$; $P = 0.04$; 9 to 15°C). Air temperatures (maximum, minimum, and average) were not correlated with CS severity (Table 5). However, the number of days with air temperature $\geq 30^\circ\text{C}$ had a significant effect on CS incidence and severity during M3 and M4 after seeding. More days with air temperature $\geq 30^\circ\text{C}$ were recorded in 2005 (38) and fewer in 2004 (4) and 2009 (4). The number of days with air temperature $\geq 30^\circ\text{C}$ were negatively correlated with CS incidence during M3 ($r = -0.75$ at $P = 0.03$; 1 to 11 days) and M4 AP ($r = -0.71$ at $P = 0.04$; 0 to 5 days), and with CS severity during M3 AP ($r = -0.81$ at $P = 0.01$; 1 to 11) and M4 AP ($r = -0.74$ at $P = 0.03$; 0 to 5 days) (Table 5). On average and over the 8 years, 4 days with temperature $\geq 30^\circ\text{C}$ during M2 (Fig. 1E and F) and 6 days during M3 (Fig. 1G and H) were sufficient to reduce CS incidence and severity.

Total rainfall in the growing season was also influential in CS development, particularly during M2 (Fig. 1A and B) and M3 (Fig. 1C and D) after seeding. A strong and positive correlation between rainfall and CS incidence ($r = 0.91$ at $P = 0.001$) and severity ($r = 0.88$ at $P = 0.003$; 22 to 135 mm) was found during M2 after seeding. There was also a relationship between rainfall and CS severity

Table 3. Cavity spot severity (disease severity index [DSI]) on colored carrot cultivars grown on organic soil at the Muck Crops Research Station, Holland Marsh, Ontario, between 2005 and 2009^a

Cultivar	Color	DSI									
		2005		2006		2007		2008		2009	
		Mid ^y	Post ^z	Mid	Post	Mid	Post	Mid	Post	Mid	Post
Purple Haze	Purple	1.8 ns	4.4 a	4.5 a	1.6 a	6.4 ns	5.3 ab	8.8 a	5.3 a	9.1 a	4.5 a
Purple Rain	Purple	...	...	...	...	4.8	2.7 a	16.6 ab	9.8 ab	...	...
Cosmic Purple	Purple	3.8	28.9 c	5.1 a	23.0 bc	3.2	15.0 ab	29.7 bc	46.8 e-g	...	...
Cellobunch	Orange	0.6	9.7 a	11.4 ab	8.8 ab	15.6	14.3 ab	23.0 a-c	26.9 a-e	25.1 ab	31.4 b
YaYa	Orange	1.5	14.2 ab	10.2 ab	15.4 ab	4.8	8.8 ab	17.1 ab	32.2 b-f	...	...
Alpha Better F1	Orange	...	...	...	...	13.3	8.0 ab	34.7 bc	44.6 d-g	...	...
Envy	Orange	...	...	...	...	10.7	7.3 ab	20.5 a-c	31.2 a-f	21.3 ab	43.1 bc
Atomic Red	Red	0.5	43.6 d	10.4 ab	50.2 d	3.5	23.9 bc	20.1 a-c	54.0 f-g	51.7 d	71.4 d
Indian	Red	...	...	...	...	16.5	38.7 c	23.0 a-c	40.4 c-g	...	...
Proline Red	Red	...	...	...	...	...	...	34.2 bc	65.9 g	...	...
Dragon	Red	1.3	31.0 c	6.7 a	31.7 c	...	...	23.9 a-c	47.9 e-g	...	...
White Satin	White	...	...	...	10.4 ab	11.6	25.9 a-c	42.1 c-g	31.2 bc	50.3 c	...
Belgium White	White	0.8	8.5 a	13.0 ab	14.4 ab	...	...	15.9 ab	19.1 a-d	...	...
Crème de Lite	White	...	...	...	...	12.5	8.2 ab	36.9 c	34.4 b-f	...	...
Yellowstone	Yellow	0.0	7.6 a	9.0 a	21.3 bc	...	...	22.6 a-c	16.4 a-c	...	...
Amarillo Yellow	Yellow	2.0	5.4 a	8.5 a	18.9 bc	...	...	18.8 a-c	22.2 a-e	...	...
Mellow Yellow	Yellow	1.8	21.7 bc	24.4 b	31.1 c	10.4	13.7 ab	29.1 bc	38.1 c-f	46.9 cd	47.4 c
Rainbow	Mixed	3.5	10.7 a	15.4 ab	19.5 bc	...	...	...	...	...	...

^a DSI = $[\sum(\text{class number}) \times (\text{number of roots in each class})] / (\text{total number of roots} \times \text{number classes} - 1) \times 100$, equation adapted from Kobriger and Hagedorn (22). Severity classes where class 0 = no lesions, class 1 = lesions of 0 to 0.9 mm, class 2 = lesions of 1 to 2 mm, class 3 = lesions of 2 to 5 mm, class 4 = lesions of 5 to 10 mm, and class 5 = lesions >10 mm. Numbers in a column followed by the same letter were not significantly different at $P \leq 0.05$; ns denotes not significantly different at $P \leq 0.05$, based on Turkey's Studentized range (honestly significant difference) test.

^y Mid = midseason, 11 or 12 weeks after planting. Carrot roots ($n = 25$ per replication) were hand harvested and evaluated for cavity spot incidence and severity.

^z Post = postharvest. Carrot roots ($n = 50$ per replication) were harvested and kept in a cold storage ($1 \pm 1^\circ\text{C}$; relative humidity of $95 \pm 2\%$) for 4 to 6 weeks postharvest and assessed for cavity spot incidence and severity.

($r = 0.70$ at $P = 0.05$; 18 to 93 mm) during M3 but CS incidence was not correlated with total rainfall (Table 5).

Stepwise regressions. To further explore the effect of weather variables that might influence the development of CS, multiple regression equations were developed using all weather parameters and incidence and severity data. The postharvest data from all 23 pigmented carrot cultivars and breeding lines were included. The best predictors for DI and disease severity were total rainfall and soil temperature within 20 cm of depth. Total rainfall during M2 was the single common factor affecting both incidence and severity (Table 6). Total rainfall during M3 also affected CS severity. Soil temperature averages of 5-, 10-, and 20-cm depths during M1 AP and the soil temperatures at the 10-cm depth during M5 were related to CS incidence, while soil temperature at the 20-cm depth was related to CS severity. With these results, CS incidence is best predicted by the regression model $DI = 166.92 - 6.524 \times$ [(average soil temperature averaged over 5, 10, and 20 cm of depth M1) + $1.982 \times$ (total rainfall M2) - $5.109 \times$ (soil temperature at 10 cm of depth M5)] ($R^2 = 1.00$ at $P = 0.005$). For CS severity, the best model is $DSI = 165.11 + [1.503 \times$ (total rainfall M2) - $0.289 \times$ (total rainfall M3) - $7.993 \times$ (soil temperature at 20 cm of depth M3)] ($R^2 = 1.00$ at $P = 0.004$).

Discussion

The severity of CS was studied over a period of 8 years in relationship to cultivars with different pigments and weather parameters. Although all cultivars had some symptoms of CS, the purple breeding line USDA 106-3 and cultivars Purple Haze and Purple Rain consistently exhibited high levels of resistance. The orange carrot cultivars were intermediate in their susceptibility to CS,

while the red breeding line USDA 104-3 and red cultivars Atomic Red, Proline Red, and an unnamed carrot from India were very susceptible to CS. The susceptibility of the yellow and white cultivars was variable but was generally less than that of the red cultivars.

The role of plant pigments in carrot and other vegetables in preventing certain human cancers has been investigated (4,6,9,10,37). However, this is the only study to investigate the relationship between pigmented carrot cultivars and a plant disease, although pigmentation has been associated with disease resistance in other crops, such as onion (34). Studies on plant defense mechanisms against fungal diseases indicate that plant phenolics, which are also associated with darker pigmented vegetables, appear to play a significant role in reducing the appearance and size of CS lesions (15). There may be an association between the intensity of the purple pigments and phenol content, which might relate to CS resistance. However, the purple carrot Cosmic Purple was among the cultivars with moderate to high susceptibility to CS; thus, the role of purple pigments in disease resistance remains unclear. Existing genetic differences among purple carrot cultivars such as intensity of the pigments, the thickness or depth of the outer layer, and the core color of each cultivar may affect the development and visibility of CS lesions. These genetic differences may also affect the phenolic content in each cultivar and, consequently, influence resistance to CS.

Differences observed in CS susceptibility among cultivars were also reflected in lesion length and depth. Lesion differences may be attributed to the different *Pythium* spp. associated with CS and their biology, growth rate, and interaction with the carrot. Studies suggest that some *Pythium* spp. invade and deeply penetrate the

Table 4. Average air temperature, total rainfall, number of days with air temperature $\geq 30^\circ\text{C}$ and number of days with rainfall during the growing period of carrot roots grown on organic soil at the Muck Crops Research Station, Holland Marsh, Ontario, from 2002 to 2009^w

Month	Temperature ($^\circ\text{C}$)									Rainfall (mm)								
	2002	2003	2004	2005	2006	2007	2008	2009	LTA	2002	2003	2004	2005	2006	2007	2008	2009	LTA
May	9.9	11.5	12.4	10.8	13.7	12.6	10.7	12.1	12.7	113	105	108	14	65	43	48	117	74
June	18.2	17.3	16.3	21.2	18.4	18.8	19.2	16.3	17.7	106	75	50	63	64	29	68	49	74
July	15.2	20.0	19.3	21.8	21.9	19.2	20.4	17.7	20.1	76	29	102	33	72	27	137	135	83
August	19.6	20.4	17.9	19.9	19.2	19.7	17.9	19.1	19.1	18	81	104	56	41	22	63	89	80
September	17.5	15.0	16.7	16.8	14.3	16.2	14.7	14.7	14.9	40	111	25	53	174	40	82	51	83
October	7.3	8.0	9.1	10.0	7.9	12.5	7.4	7.4	8.6	49	78	26	41	102	32	54	62	67
Total ^x	...	...	...	...	...	...	...	...	...	402	478	416	260	518	193	452	503	461
Days $\geq 30^\circ\text{C}$ ^y	34	15	4	38	19	26	16	4	...	...	...	...	...	...	...	...	...	...
Days ≥ 2.5 mm ^z	...	...	...	...	...	...	...	...	...	52	63	57	40	63	36	24	29	...

^w Temperature and rainfall data were collected at a weather station located on organic soil at Muck Crops research Station, Holland Marsh, Ontario. LTA = 10-year averages (29).

^x Total = total rainfall during the growing season.

^y Total days with temperature $\geq 30^\circ\text{C}$.

^z Total days with rain ≥ 2.5 mm.

Table 5. Linear correlations between cavity spot incidence (disease incidence [DI]) and severity (disease severity index [DSI]) on 22 colored carrot breeding lines or cultivars and weather variables evaluated on organic soil at the Muck Crops Research Station, Holland Marsh, Ontario, from 2002 to 2009^v

Weather variables ^v	Name	MAP ^z	DI ^w		DSI ^x	
			r	P	r	P
Total rainfall (mm)	TR	M2	0.91	0.001	0.88	0.003
		M3	ns	ns	0.70	0.05
Mean maximum air temperature ($^\circ\text{C}$)	T Max	M4	-0.69	0.05	ns	ns
Mean minimum air temperature ($^\circ\text{C}$)	T Min	M5	-0.71	0.04	ns	ns
Number of days with air temperature $>30^\circ\text{C}$	T $> 30^\circ\text{C}$	M3	-0.75	0.03	-0.81	0.01
		M4	-0.71	0.04	-0.74	0.03

^v Significant correlations at $P \leq 0.05$; ns = not significant.

^w DI = percent carrot roots with lesions.

^x $DSI = [\Sigma(\text{class number}) \times (\text{number of roots in each class})] / (\text{total number of roots} \times \text{number classes} - 1) \times 100$, equation adapted from Kobriger and Hagedorn (22). Severity classes where class 0 = no lesions, class 1 = lesions of 0 to 0.9 mm, class 2 = lesions of 1 to 2 mm, class 3 = lesions of 2 to 5 mm, class 4 = lesions of 5 to 10 mm, and class 5 = lesions >10 mm.

^y Weather data were collected each year during the growing period (May to October or November) at automated weather stations located near the research trials at the Muck Crops Research Station (weather station located approximately 200 m from carrot plots). Daily weather parameters were averaged and grouped by months (month one to month five = M1 to M5) after seeding the trials each growing season.

^z Number of months after planting ($n = \text{M1 to M5}$).

carrot root while others remain at the root surface, consequently causing different lesion types (i.e., length and depth; 5,15). CS in these trials was caused by the same *Pythium* spp. isolated and associated with the disease at this site in 1994 (28); in particular, *P.*

violae and *P. ultimum*. In this study, CS lesions were generally fewer and smaller at the midseason evaluations compared with those postharvest. These observations are in agreement with those of Maynard et al. (27) and Montfort and Rouxel (30), who found

Fig. 1. Effect of total rainfall and number of days with air temperatures $\geq 30^\circ\text{C}$ during months two (M2) and three (M3) after planting on cavity spot **A, C, E, and G**, incidence (DI) and **B, D, F, and H**, severity (DSI) of pigmented carrot breeding lines ($n = 5$) and cultivars ($n = 18$) evaluated between 2002 and 2009.

an increase in CS lesion number and size per root with increasing plant age.

An increase in the size of lesions for most cultivars was observed as the season progressed but, for some orange, purple, and yellow cultivars, the severity of CS was high early in the growing season (midseason assessment) and lower postharvest. These changes are consistent with the findings of Suffert and Guibert (41), Suffert and Montfort, (42,43) and Suffert et al. (44), who studied the mechanisms of carrot infection by *Pythium* spp. and CS field epidemics. These studies also complemented earlier findings by Phelps et al. (36) suggesting that initial infection of carrot by *Pythium* spp. could result in secondary and tertiary infection of the same root. CS epidemics follow classical epidemiological phases driven by successive processes during root infection (42,44). There is a phase in which the pathogen inoculum in the soil leads to primary infection, a phase of pathogen spread to adjacent taproots (alloinfection), and a phase of intensification of the pathogen infection on the same tap root (autoinfection). The results of this study indicate that both alloinfection and autoinfection processes occurred in muck soils, and that cultivars responded differently to the two infection processes. Some cultivars were more prone to autoinfection than alloinfection, and this was the case of for Atomic Red, Cosmic Purple, and the unnamed Indian cultivar, which showed an increase in CS severity between midseason and postharvest evaluations. Following infection from *Pythium* spp. inoculum in the soil, the pathogen produced secondary inoculum which was released into the soil and which caused more lesions on the same root. Conversely, orange Cellobunch and 'YaYa' appear to be more prone to alloinfection rather than autoinfection, because their CS severity was high early in the evaluations and declined or remained at the same level by harvest, according to postharvest assessments. In this case (alloinfection), it is suggested that only the inoculum from the soil is effective in causing lesions and there is little or no increase in inoculum or autoinfection thereafter. The purple cultivars Purple Rain and Purple Haze had low disease severity throughout the season.

One point that has not been investigated is whether some CS lesions shrink or disappear over time. Lesions on foliage induced by foliar pathogens tend to remain the same or increase in size (13,46). However, roots and tubers produce callus tissue to wall off wounded tissue or halt infection and it is possible that, once lesion expansion is halted, the lesion appears smaller as the root enlarges and grows around it, or that small lesions become so small that they are no longer visible (3,5,15).

There were similarities in CS susceptibility and severity among some carrot breeding lines and cultivars. The purple breeding line USDA 106-3 and the purple cultivars Purple Haze and Purple Rain were relatively resistant to CS, while the red breeding line USDA 104-3 and the cultivars Atomic Red, Proline Red, and the unnamed carrot from India were susceptible to CS.

Among the weather parameters evaluated, total rainfall was most closely correlated with CS. The disease levels were higher in years

with rainfall above 400 mm during the growing season and lower in years with 260 mm or less total rainfall. Regardless of rainfall amounts, the time after planting carrot lines when the rain events took place was more important in CS development. Rain during M2 and M3 after seeding had the greatest influence.

In contrast, and as expected, high maximum and minimum air temperatures were associated with low CS. This negative relationship was stronger when there were more days in the growing season with temperatures $\geq 30^{\circ}\text{C}$. High temperatures and low precipitation during the dry growing seasons of 2005 and 2007 are most likely responsible for the low CS levels recorded in these years.

Rainfall influences soil moisture and air temperature affects soil temperature throughout the growing season. The influence of soil moisture and temperature on the severity of diseases caused by *Pythium* spp. and the frequency of different *Pythium* spp. in soils has been studied on carrot and many other host plants. For alfalfa, soil moisture, through rainfall or irrigation, was more important for increase and infection by the *Pythium* spp. that formed zoospores but did not have much effect on *P. ultimum* and *P. irregulare* (17).

A CS study in British Columbia identified an association between soil moisture, flooding, and soil temperatures of 15°C and optimal disease development (3). The highest disease occurred as a result of infections after high precipitation, primarily between 4 and 12 weeks after planting. This is quite consistent with the M2 and M3 after planting that were found to be most important in the present study. In another study, carrot roots inoculated with different *Pythium* spp. had more CS lesions when plants were frequently irrigated (35). Several others have also reported an increase in CS associated with high soil moisture, flooded soils, or poor drainage and low temperature (13,28,40,46). Suffert et al. (44) reported that a deficit of soil moisture limited the movement of *Pythium* propagules to host tissue, thus reducing primary infections in the field. This also promoted healing of lesions and limited lesion expansion and the potential for alloinfection. In this study, it was observed that CS was initiated when mean air temperatures were between 10 and 15°C and that disease was low at temperatures $\geq 18^{\circ}\text{C}$, and is in agreement with other field studies (14,26,35,40,46). McDonald (28) reported that soil temperatures of 16 and 17.5°C during the 6 to 8 weeks after seeding was associated with high CS incidence, and Vivoda et al. (46) reported more CS at 15 than at 20 or 25°C . Kerns and Tredway (20) reported that *P. volutum* was most active and more root infection occurred when soil temperatures were between 12 and 24°C , although this *Pythium* sp. is not usually associated with CS.

Stepwise regression of the weather parameters indicated that total rainfall during M2 and M3, soil temperature at 10 cm of depth during M1 and M5, and soil temperature at 20 cm of depth during M3 were the variables that best predicted CS incidence and severity. This is consistent with carrot development and growth and development of *Pythium* spp. The marketable portion of the carrot root develops within the top 20 cm of soil and the expansion of the

Table 6. Best-fitting regression equation for describing the relationship between cavity spot incidence (disease incidence [DI]) and severity (disease severity index [DSI]) on 23 colored carrot breeding lines or cultivars evaluated on organic soils at the Muck Crops Research Station, Holland Marsh, Ontario, from 2002 to 2009^z

Step	Parameters and equations	Partial R^2	Model R^2	F value	Pr > F
DI ^z					
1	Total rainfall during month two (TRM2)	0.6960	0.6960	6.87	0.0790
2	Soil temperature at 10 cm depth during month five (ST10cm M5)	0.2817	0.9777	25.29	0.0373
3	Average soil temperature 5–20cm depth during month one (STAV M1)	0.0223	1.00	1,682.19	0.0155
Equation	DI = $166.92 - 6.524 \times \text{STAV M1} + 1.982 \times \text{TRM2} - 5.109 \times \text{ST10cm M5}$	...	...	...	...
DSI ^z					
1	Total rainfall during month two (TRM2)	0.7112	0.7112	7.39	0.0727
2	Total rainfall during month three (TRM3)	0.2756	0.9858	41.62	0.0232
3	Soil temperature at 20cm depth during month three (ST20cm M3)	0.0132	1.00	1,312.58	0.0176
Equation	DSI = $165.11 + 1.503 \times \text{TRM2} - 0.289 \times \text{TRM3} - 7.993 \times \text{ST20cm M3}$	...	...	...	...

^z Carrot breeding lines USDA 106-3, USDA 104-3, USDA 101-23, USDA 105-7, and USDA 102-1 and carrot cultivars Cellobunch, Dragon, Atomic Red, Mellow Yellow, YaYa, Envy, Cosmic Purple, Purple Haze, Purple Rain, Indian, Proline Red, Yellow Stone, Amarillo Yellow, Crème de Lite, White Satin, Belgium White, Alfa Better F1, and Rainbow were evaluated for cavity spot incidence and severity between 2002 and 2009.

tap root begins between M2 and M3. This is also the period of high susceptibility of carrot to root infection (11,28).

The relationship of weather parameters to CS will allow growers to plan disease management strategies such as modifying irrigation or harvest dates to limit CS and increase the volume of marketable carrot roots.

This is the first study in which colored carrot breeding lines and cultivars were evaluated for reaction to CS over several years. Several purple-pigmented cultivars were found to be highly resistant to CS, while several red cultivars were very susceptible. Standard orange cultivars tended to be moderately susceptible. It is not known if the pigments affect *Pythium* spp. during CS development, particularly when phenolics, the first line of a plant's defense mechanism, are produced in large quantities. These interactions should be further investigated. Also, comparative studies with pigmented carrot cultivars from different genetic sources are further required to explain, for example, whether differences in the pigments in purple carrot are responsible for the different responses to CS.

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